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Misperceptions of speed for chromatic and luminance grating stimuli

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Abstract

Errors in the perception of speed of moving visual stimuli can occur when presented stimuli are of unequal contrast and when they appear alongside additional modifier stimuli that move at different speeds. We have examined these misperceptions for chromatic and luminance grating stimuli in order to assess to what extent these different kinds of motion cue might be utilised in the analysis of speed of moving objects. We show that the dependence on contrast of speed matching for luminance and chromatic stimuli is similar over a range of stimulus speeds greater than 4 deg/s. Differences between the contrast dependencies of speed perception for chromatic and luminance stimuli are only evident at slow speeds (< 4 deg/s) and low contrasts. The presence of modifier stimuli can directly influence the perceived speed at both high and low velocities and contrasts. This influence was found to be independent of the modifiers' chromaticity and was greatest when the modifiers were adjacent to and presented simultaneously with the test and reference stimuli. However, the modifiers were still able to induce measurable changes in perceived speed for increased separations over space and time. Taken together these results indicate that whilst differences do exist in the contrast dependencies of speed perception for chromatic and luminance stimuli, they are evident only for a narrow range of stimulus parameters (i.e. low speed and low contrast). There appears to be ample scope for interactions between chromatic and luminance contrast in speed perception where there is the capacity to pool this information over a relatively broad spatio-temporal extent.

Keywords: Speed perception; Motion psychophysics; Colour; Luminance

1. Introduction

It is well known that the human visual system can misperceive the speed of moving stimuli under certain conditions. For example, the perceived speed of a grating stimulus is highly dependent upon contrast (Anstis, 2003; Blakemore & Snowden, 1999; Gegenfurtner & Hawken, 1996a, 1996b; Hawken, Gegenfurtner, & Tang, 1994; Johnston, Benton, & Morgan, 1999; Stone & Thompson, 1992; Thompson, 1982; Thompson, Brooks & Hammett, 2006). Such misperceptions can be observed when the stimuli are separated either in space or time (Thompson, Stone, & Swash, 1996) and appear to be more pronounced for slow as opposed to fast moving stimuli (Johnston et al., 1999; McKee, Silverman, & Nakayama, 1986). The perceived speed of a stimulus is also dependent upon the context within which it is viewed. Smith and Derrington (1996) have shown how the perception of speed of a moving test grating can be altered by the presence of additional gratings moving at different speeds placed in close proximity. These so-called 'modifier' stimuli induce a reduction in perceived speed when they move more slowly than the stimulus under consideration, but lead to an increase in the perceived speed when they move faster.

Early ideas as to how the visual system extracted information about the speed of moving stimuli suggested computations based on the relative activities of at least two spatiotemporal filters tuned to different temporal frequencies (Foster, Gaska, Nagler, & Pollen, 1985; Smith & Edgar, 1994; Watson & Ahumada, 1985). Outputs from these filters may also undergo an additional contrast normalisation stage in which filter outputs are divided by average contrast (Adelson & Bergen, 1986). However, a major

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problem with such ratio models is that they predict contrast invariant speed estimations; any increase in filter output due to increased contrast should affect all filters equally, with no effect on the output ratio. In an attempt to explain observed misperceptions of speed with contrast, (Stone & Thompson, 1992) proposed a modified version of contrast normalisation in which the sampling of spatial contrast takes place over an area larger than that over which motion energy is sampled. Thus, if two grating stimuli, one of high contrast and the other low, are presented simultaneously moving at the same speed, then the motion energy signal from the high contrast stimulus would be normalised by an inappropriately low average contrast value and as a result would be perceived as moving faster. On the other hand, motion energy from the low contrast stimulus would be normalised by a high average contrast and would thus appear to move more slowly than it actually does. This normalisation process occurs for motion signals derived from stimuli that are similar in terms of their direction and takes place across a limited temporal window (Stone & Thompson, 1992). However, it cannot provide a complete explanation because the pattern of speed misperceptions generated by modifiers in the experiments of Smith and Derrington (1996) should not occur if speed estimates are normalized by average contrast alone, as modifier temporal frequency should have no effect on speed percept. This suggests that perceived speed also depends upon the ratio of low and high temporal frequency signals that are averaged over regions of the visual field (Smith & Derrington, 1996). More recent attempts at modelling speed perception continue to employ an estimate of speed based upon the ratio of outputs from low- and band-pass temporal filters (Perrone, 2004, 2005) which is taken after the signals are modified by separate non-linear transducers (Thompson, Brooks, & Hammett, 2006).

The physiological basis of speed perception has been a focus of attention in vision research over recent years. Key elements of these mechanisms are neurons, located in area V5/MT, that are selectively responsive to stimulus speed (Liu & Newsome, 2005; Perrone & Thiele, 2001; Priebe & Lisberger, 2004). Crucially, the responses of these neurons are unaffected by changes in the spatial and temporal frequency composition of stimuli and, unlike V1 neurons, they appear to be able to truly represent retinal image speeds, as opposed to their temporal frequency content. However, recent studies have questioned the role of these neurons in speed perception as they have been found to constitute only a minority of neurons responsive to speed in area V5/MT (Priebe, Casanello, & Lisberger, 2003). Whilst it is clear that the operation of speed selective neurons allows them to disregard the pattern content of stimuli in the estimation of their speed (Perrone & Thiele, 2001), it has yet to be demonstrated whether they are able to disregard information that might be derived from different types of motion cue. For example, would these speed neurons respond in the same manner to motion defined by spatio-temporal changes in luminance as they would to motion defined purely by changes in colour or wavelength? This question as to how luminance- and chromatically defined motion are analysed by the visual system has a long history in vision science. Traditional models posit that colour and luminance motion stimuli are analysed within segregated pathways localised within different regions of the cerebral cortex (e.g. Livingstone & Hubel, 1987; Zeki, 1978). In this strictly parallel model of visual processing, motion that is defined by spatio-temporal changes in colour presents something of a problem, namely, is it processed by a separate cortical network specialised for colour, or by a network specialised for the analysis of motion? Some experimental findings have championed segregation. As discussed above, the perceived speed of a moving stimulus is highly dependent upon its contrast, with higher contrast stimuli appearing to move faster than lower contrast ones (Anstis, 2003; Blakemore & Snowden, 1999; Gegenfurtner & Hawken, 1996a; Hawken et al., 1994; Johnston et al., 1999; Stone & Thompson, 1992; Thompson, 1982; Thompson et al., 2006). Crucially, Hawken et al. (1994) highlighted the fact that the dependency on contrast of these misperceptions was very different for colour and luminance defined motion stimuli, the former being highly dependent upon contrast in comparison to the latter. These differences led to the proposal that, at least for slow moving stimuli, the analysis of colour and luminance motion occurs within separate processing pathways (Burr, Fiorentini, & Morrone, 1998; Hawken et al., 1994). However, other results from neurophysiological experiments strongly challenge this strict segregationist view and instead promote the idea that colour and luminance motion perception is based upon a common neural mechanism (Barberini, Cohen, Wandell, & Newsome, 2005; Cavanagh & Anstis, 1991; Cavanagh & Favreau, 1985; Dougherty, Press, & Wandell, 1999; Seidemann, Poirson, Wandell, & Newsome, 1999; Wandell et al., 1999).

These conflicting views have obvious implications relating to how colour and luminance defined motion cues can be utilised in the analysis of stimulus speed. Certainly, the ability to utilise and integrate information across these different sub-modalities would seem to be more consistent with the physiological properties of speed sensitive neurons in area V5/MT (Perrone & Thiele, 2001). Therefore a fundamental question we wish to address here is to what extent colour and luminance contrast can be combined or segregated in the estimation of stimulus speed. To do this we propose to examine the contrast dependencies of chromatic and luminance speed perception paying close attention to two important factors that have been highlighted as potential sources of the conflicting findings in the studies highlighted above: (1) that comparisons of performance are made across comparable contrast ranges for colour and luminance stimuli (Dougherty et al., 1999). (2) That chromatic and luminance speed perception is compared for slow (<4 deg/s) as well as fast moving stimuli (Johnston et al., 1999). By paying close attention to these factors we

wish to re-assess the case for the proposal that colour and luminance defined motion are processed by separate pathways.

Perceived speed is also dependent upon the context within which it is viewed. Smith and Derrington (1996) have shown that high contrast 'modifier' stimuli placed in close proximity to a test stimulus can influence its perceived speed. For example, when the modifiers move faster than the test stimulus, the test is perceived as moving more quickly than its actual speed, and when the modifiers move slower, the test is then perceived as moving more slowly. In the light of these findings, which have hitherto been restricted to the use of only luminance contrast motion stimuli, we wish to address the issue of whether the colour or luminance composition of modifier stimuli has any influence on the pattern of results reported by Smith and Derrington. Could, for example, equiluminant colour modifiers bias the perceived speed of achromatic contrast test stimuli, and vice versa? If induced misperceptions of speed turned out to be the same regardless of the chromatic or luminance contrast composition of the modifier and test stimuli, it would be strong evidence in favour of the idea that speed perception, rather than relying upon segregated colour and luminance input, is based instead upon mechanisms which pool motion energy from different inputs, the contrast composition of which (i.e. chromatic or luminance) is ignored.

2. Methods

2.1. Stimuli

Moving chromatic and luminance grating stimuli were presented on a high-resolution colour graphics monitor (GDM500; Sony, Tokyo, Japan; frame rate 120 Hz) controlled via a video graphics card (VSG 2/5; Cambridge Research Systems, Rochester, UK). The gratings were vertically oriented 1 cycle/deg sinusoidal stimuli which were presented in square windows of side 2.5° displaced by a total of 3.75° above and below a central fixation point. They appeared on a grey (illuminant C) background of mean luminance equal to 12.5 cd/m^2.

Chromaticity of the reference and test stimuli could be independently controlled so as to produce chromatic modulations along a series of axes in DKL colour space (Derrington, Krauskopf, & Lennie, 1984). L-, M- and S-cone modulation can be varied in this space by variation of azimuth (ϕ) in the equiluminant plane. Two main axes of modulation were used for the chromatic stimuli, a 0–180° or L–M axis which modulates only L- and M-cones and minimally activates S-cones (1931 CIE chromaticity co-ordinates: $x_0 = 0.3819$, $y_0 = 0.2826$, $x_{180} = 0.238$, $y_{180} = 0.3494$). The second, 90–270° or S − (L + M) axis, modulates only the S-cones, keeping L- and M-cone activation constant ($x_{90} = 0.2724$, $y_{90} = 0.228$, $x_{270} = 0.348$, $y_{270} = 0.404$). A third axis with modulation along elevation, $\theta = \pm 90°$ was used to generate luminance (achromatic, L + M) contrast stimuli. Calibration of stimuli in all experiments was performed using a PR650 Spectrascan SpectraColorimeter. Individual isoluminant points were obtained using a minimum motion technique (Anstis & Cavanagh, 1983) and heterochromatic flicker photometry (HFP) in the exact positions as they were to be presented for the speed matching experiments and in the modifier matching experiments. One potential area of concern was that the chromatic stimuli, particularly those of high contrast, might contain significant artefactual luminance signals, despite having performed HFP. However, in control experiments detailed elsewhere (McKeefry, Laviers, & McGraw, 2006) we have shown that there is minimal cross adaptation between colour and luminance grating stimuli in the generation of motion after-effects across a large contrast range. This tends to argue against the presence of luminance signals contaminating erstwhile high contrast chromatic stimuli. All chromatic and luminance contrast stimuli were equated with reference to their respective motion detection thresholds, which were measured in preliminary experiments using a temporal 2AFC procedure for all stimuli at the specific velocities used.

2.2. Psychophysical procedure

Speed matching experiments were conducted using a self-paced two alternative forced choice (method of constant stimuli) paradigm to obtain a psychometric function. During each trial a superior (test) and inferior (reference) grating were presented simultaneously for 0.833 s whilst observers maintained fixation on a central spot. The reference grating always moved at a constant velocity (2, 3, 8, 12 or 16 deg/s, depending on the experiment). The test stimulus was presented randomly at one of seven different speed levels which spanned a range (±36%) above and below the reference speed with each stimulus being presented a minimum of 30 times. The suitability of this range for all reference stimuli was verified in preliminary experiments. The test and reference stimuli moved in opposite directions in order that tracking eye movements were minimised. Following presentation of the stimuli observers were required to indicate, via a response box (model CB3; Cambridge Research Systems) which grating moved faster. Observers were given no feedback as to the correctness or otherwise of their response during the test.

Bootstrap analysis (Bootstrap program Version 2.4 (1996); Foster & Bischof, 1991) was used to generate psychometric curves from the data and identify the perceived speed required to match the speed of the reference grating (point of subjective equality) where the test or reference were equally likely to be designated as moving faster. This matching speed was then converted to a measure of relative speed given as: relative speed = (reference speed/matching speed) × 100. Relative speed was then plotted against log test/reference contrast ratio and the slope of regression lines fitted to these data gives a measure of the contrast dependency or gain. Contrast ratio was always expressed in relation to a specific reference stimulus supra-threshold level. For example, if the reference contrast was 2.5× threshold then a contrast ratio of 4 would mean the test stimulus had a contrast of 10× threshold, a ratio of 0.25 would mean the test stimulus had a contrast of 0.625× threshold.

Two main groups of experiments were performed. The first, speed matching experiments, involved observers making speed matches between test and reference stimuli which either contained modulations along the same (homogenous speed matching) or different (heterogeneous speed matching) chromatic axes in colour space. The second group, modifier speed matching experiments, in essence were similar to the previous paradigms, with the exception that the speed matches were made in the presence of modifier stimuli located at either side of the reference stimulus. These were identical in size to the test and reference (see Fig. 1b) and consisted of luminance, L–M or S − (L + M) gratings of different contrasts which moved in the same direction as the reference. The basic speed matching trial was repeated in the presence of these modifiers which had the same initial spatial phase as the reference stimulus. Trials conducted were with the modifiers moving at 0, 1.5, 3, 4.5 and 6 deg/s, when the reference was moving at 3 deg/s; and 0, 3, 6, 8, 10, 13 and 16 deg/s when the reference was moving at 8 deg/s. In all experiments the luminance and chromatic stimuli (test, reference and modifiers) were expressed as multiples above their respective motion detection thresholds.

The appearance of the modifiers relative to the test and reference stimuli could be manipulated in both space and time. In the initial experiments the modifiers directly abutted the reference stimuli and were temporally coincident. Subsequent experiments examined the effects of increasing the spatial separation between the reference and modifiers by moving the latter to more peripheral (equidistant) horizontal locations. We also examined the effects of temporal separation by introducing a stimulus onset asynchrony (SOA) between the modifier and the test/reference

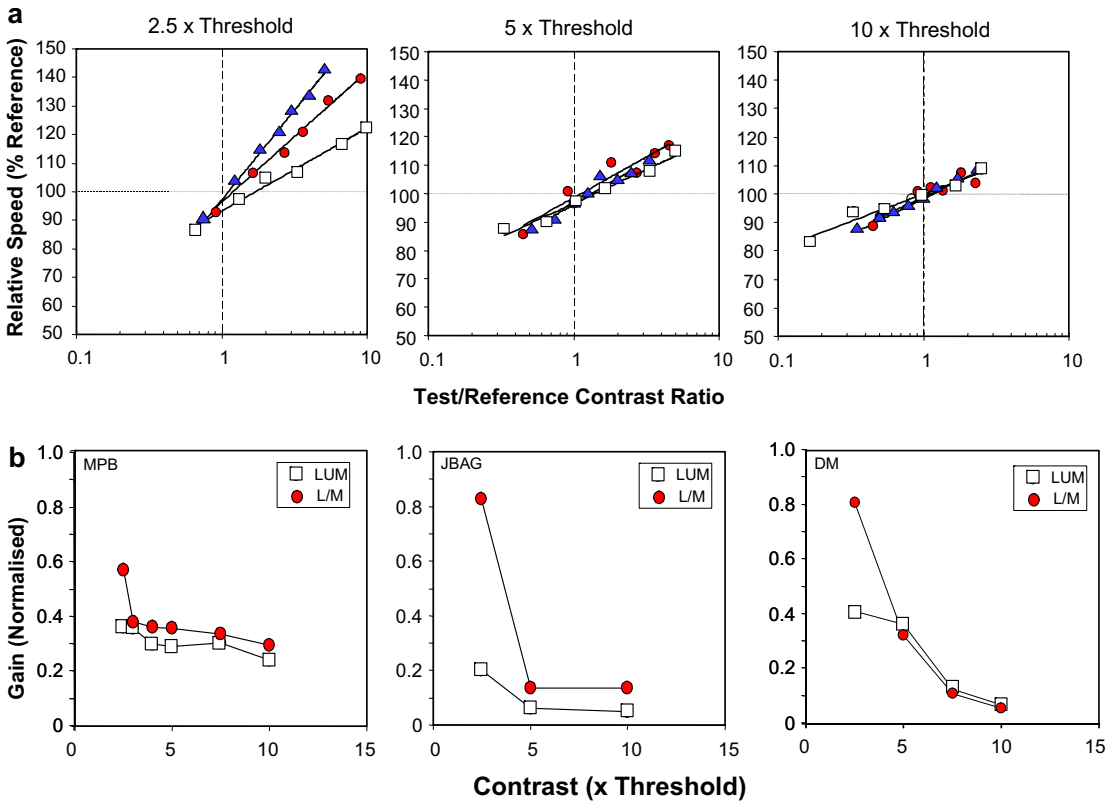

Fig. 1. (a) Speed matching functions for luminance (squares), L–M (circles) and S/(L + M) (triangles) gratings at 2.5×, 5× and 10× motion detection threshold. Observer MPB. (b) Contrast gain of speed matching for luminance (squares) and chromatic L/M (circles) grating stimuli plotted as a function of stimulus contrast. Observers: MPB, JBAG and DM.

appearance, which could be negative (i.e. the modifiers appeared before the test and reference) or positive (i.e. the modifiers appeared after the test and reference).

2.3. Subjects

Experiments were conducted by four male observers (mean age 29 yrs) two of whom were the authors who performed all of the experiments, the other two being naïve observers who performed specific experiments to confirm key findings. All subjects were colour normal according to the Farnswoth-Munsell 100 Hue and City University colour vision tests and were corrected to 6/6 or better with appropriate visual correction. All observers were experienced in psychophysical observation. Subjects viewed the display binocularly with normal pupils and mild head restraint which maintained a viewing distance of 114 cm.

3. Speed matching experiments

3.1. Homogeneous speed matching

3.1.1. Introduction

Differences in the contrast dependency of perceived speed between chromatic and luminance stimuli have been central to the proposition that the two kinds of motion stimuli may be processed by separate pathways (Hawken et al., 1994). However, Dougherty et al. (1999) have raised the possibility that these differences arise as a result of the fact that the perceived speed of chromatic stimuli only rises sharply at high supra-threshold contrasts levels, whilst for luminance stimuli speed increases sharply just above threshold and becomes saturated at supra-threshold contrasts. Hence, they concluded that the finding of different contrast dependencies of chromatic and luminance speed perception found by Hawken and co-workers was an artefact of the restricted contrast ranges over which performance was measured. This possibility prompted us to re-examine speed matching functions for chromatic and luminance stimuli which were equated in terms of multiples above their *motion* detection thresholds. In addition, attention has been drawn to the fact that the variation of apparent speed with contrast is very much speed dependent. Slowly moving stimuli (<4 deg/s) exhibit strong variations in apparent speed with contrast, with low contrast stimuli being perceived as moving more slowly than their counterparts at high contrast. At faster rates (4–8 deg/s) speed perception is to a large extent contrast invariant (Johnston et al., 1999; McKee et al., 1986). Whilst at faster rates still (>10 deg/s) perceived speed once again varies as a function of contrast but, contrary to the observations made at slow speeds, it is low contrast stimuli that appear to move faster than high contrast stimuli (Thompson et al., 2006). Therefore, in the light of these findings it was important that we were able to compare the perception of speed for both chromatic and luminance stimuli over a range of slow and fast presentation rates.

3.1.2. Results and discussion

Fig. 1a shows typical speed matching data for 2 deg/s L/M (red–green), S/(L + M) (blue–yellow) and luminance gratings. At and above 5× motion detection threshold the slopes of the chromatic and achromatic functions are virtually identical, i.e. speed matching exhibits the same dependency on contrast for all chromatic and luminance stimuli. Only for the lowest contrasts tested (2.5× threshold) do the slopes of the matching functions become visibly different with the S/(L + M) and L/M chromatic functions exhibiting a steeper slope than their luminance counterpart. In Fig. 1b contrast dependency (gain) is plotted as a function of contrast for chromatic and achromatic stimuli for three observers who exhibit similar behaviour, in that the dependency of speed perception on contrast decreases with increasing stimulus visibility. At contrasts below 5× threshold the differences between chromatic and luminance performance is greatest, however, these differences become less marked above 5× threshold, above which the rate of change of gain falls for all stimuli.

Previous studies have highlighted the fact that dependency of speed perception on stimulus contrast changes with increasing stimulus velocity (Hawken et al., 1994; Johnston et al., 1999; Thompson, 1982). The data in Fig. 2 confirm this relationship and show that there is a reduction in contrast dependency with increasing stimulus velocity. Between 5 and 7 deg/s speed perception becomes contrast invariant for chromatic and luminance stimuli. Beyond this null region the slopes of the gain functions become negative for both colour and luminance gratings—indicating that for fast speeds lower contrast stimuli are actually perceived as moving faster than higher contrast stimuli. This finding is consistent with previous observations that have noted a similar reversal for faster moving luminance stimuli (Thompson, 1982; Thompson et al., 2006). The data presented here add to the growing body of evidence showing that the perception of speed of slowly moving gratings is highly dependent upon stimulus contrast (Anstis, 2003; Blakemore & Snowden, 1999; Gegenfurtner & Hawken, 1996a; Hawken et al., 1994; Johnston et al., 1999; Stone & Thompson, 1992; Thompson, 1982). However, this dependency diminishes, and in fact reverses for faster presentation rates which results in low contrast stimuli being perceived as moving faster than high contrast stimuli.

Earlier studies have also highlighted the existence of differences between the contrast dependencies of chromatic and luminance stimuli in the perception of speed (Gegenfurtner & Hawken, 1996a, 1996b; Hawken et al., 1994). Fig. 3 provides a summary of results from various studies (Burr et al., 1998; Hawken et al., 1994; McKeefry, 2001) that have reported similar differences between colour and luminance speed perception. The key point to note from these data is that it is only at relatively slow speeds where the differences between colour and luminance are observed. As all of the studies demonstrate, at faster rates the contrast

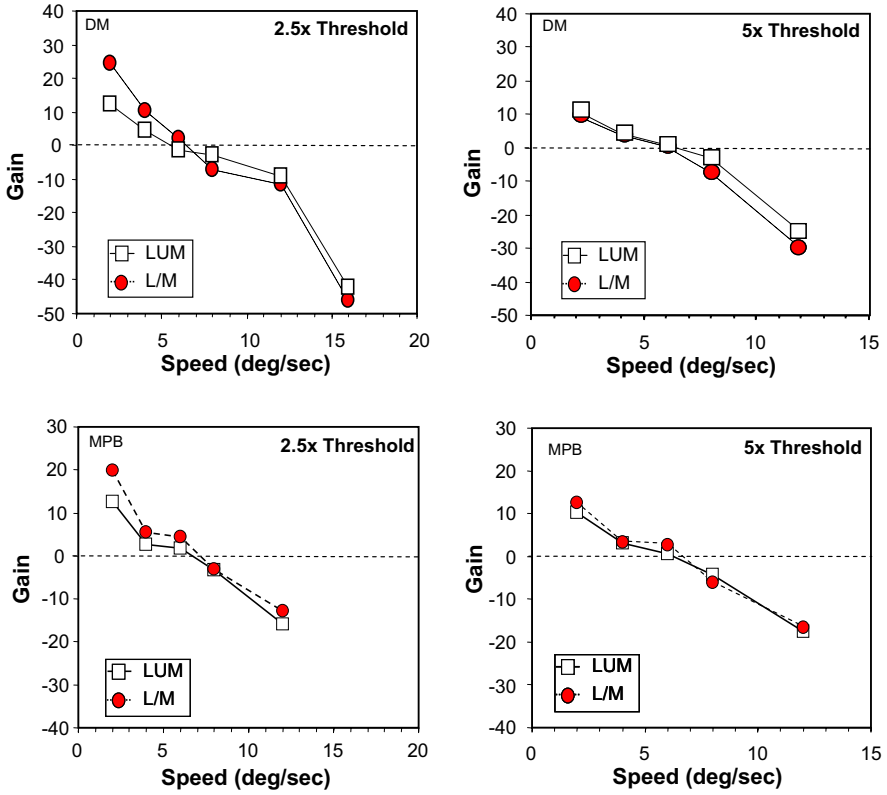

Fig. 2. Contrast gain for luminance and chromatic grating speed matching as a function of reference speed. Data are shown for relatively low (2.5×) and higher (5×) supra-threshold contrasts. Observers: MPB and DM.

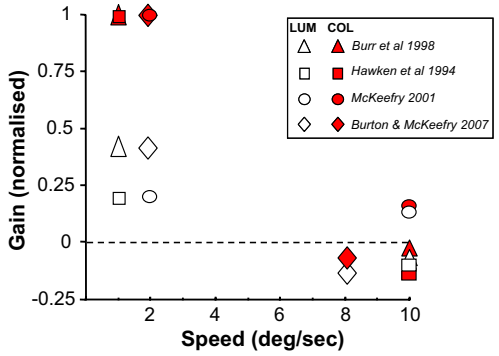

Fig. 3. Results from previous studies that have demonstrated differences in the contrast dependencies of speed perception for chromatic and luminance stimuli. Data from the current study have also been included for comparison. All of these results indicate that whist differences are apparent between colour and luminance speed perception at slow rates, these differences are reduced at faster rates.

dependencies for colour and luminance become much more similar. The results from this study (averaged across all observers) are also shown in Fig. 3 and are very much in line with these earlier findings. Crucially, the effect of contrast on speed perception changes markedly as a function of stimulus speed (see also: Johnston et al., 1999; Thompson et al., 2006). It is this change in gain with speed, as illustrated by these data, which highlights the most likely reason for the discrepancy with studies like Dougherty et al. (1999), who failed to find any differences between chromatic and luminance speed perception. Dougherty et al's stimulus was relatively fast (8.2 deg/s) and as such falls within a region where the previous studies also report little difference in gain for chromatic versus luminance stimuli.

The original description of different contrast dependencies for the speed of moving colour and luminance pattern was interpreted as being evidence for the existence of independent processing for motion defined by the two types of stimuli (Hawken et al., 1994). However, results from our experiments suggest that the differences between the perception of speed of slowly moving chromatic and luminance stimuli is not as clearly segregated as originally thought. The extent of segregation between chromatic and luminance performance is very much dependent upon the visibility of the stimulus. For moving stimuli of contrast greater than 5× their motion detection thresholds there appears to be little difference between the contrast dependencies of chromatic and luminance stimuli. Only for stimuli that have contrasts less than 5× motion detection threshold do the speed matching functions begin to exhibit observable differences in slope for chromatic and luminance stimuli. Nonetheless, even if only for a restricted range of stimulus conditions (low speed and low contrast), differences in contrast dependency do exist between chromatic and luminance stimuli. Why might such differences exist for speed perception between chromatic and luminance grating stimuli at slow rates? One possibility is that high and low speed chromatic stimuli constitute different kinds of stimuli that are processed by different visual mechanisms. Recent models of motion perception propose that the analysis of high speed (and high contrast) chromatic stimuli is performed by low-level motion energy detectors, similar to those involved in luminance motion processing. This is in comparison to low speed, low contrast chromatic stimuli which are processed by 'feature tracking' mechanisms (Cropper & Derrington, 1994, 1996; Derrington, Allen, & Delicato, 2004; McKeefry et al., 2006; Seiffert & Cavanagh, 1999). Additional support for the existence of separate processing pathways for high and low contrast chromatic stimuli comes from the finding of preserved high contrast, but impaired low contrast motion detection in human subjects suffering from cerebral achromatopsia (Cavanagh et al., 1998). Physiological evidence also points to the existence of differences in the way in which chromatic information, which changes over time, is encoded by the visual system. Lee, Martin, and Valberg (1989a) have shown that at low temporal rates (<4–5 Hz) chromatically opponent parvocellular neurons are more sensitive to chromatic flicker that their broadband magnocellular counterparts. Above 5 Hz, however, magnocellular sensitivity exceeds parvocellular sensitivity for such stimuli. Thus 4–5 Hz represents a temporal region beyond which the encoding of temporally varying chromatic information makes a transition from being mediated by parvocellular to magnocellular neurons. Moreover, this transitional region roughly coincides with that shown in our results where differences between the contrast dependencies of speed perception for chromatic and luminance stimuli become minimal.

Whilst the foregoing discussion tends to argue in favour of the existence of different pathways for the processing of motion under different stimulus conditions; colour versus luminance, high versus low contrast, fast versus slow and so forth, the question we want to answer is to what extent is this segregation reflected in the perception of stimulus speed? Are such computations performed by the visual system separately or can, for example, chromatic stimuli influence the perceived speed of luminance motion and vice versa? We will attempt to address this issue in the following experiments.

3.2. Heterogeneous speed matching

3.2.1. Introduction

The previous experiment was concerned with misperceptions of speed that occur between high and low contrast stimuli that were of the same contrast composition (i.e. luminance or chromatic). In this experiment we wished to examine whether similar misperceptions occurred between test and reference stimuli which comprise orthogonal axes in colour space, i.e. heterogeneous speed matching. As outlined earlier, a number of models have attempted to account for the perceived variations in stimulus speed that occur with changing contrast. Among these is the modified ratio model of Stone and Thompson (1992) which is based on the premise that two gratings of unequal contrast would

interfere with each others normalisation process due to the fact that spatial contrast is sampled over an area that is larger than that over which motion energy is sampled. More recent adaptations of the ratio model suggest that the relative activity of low- and band-pass temporal filters is modified by independent non-linear transducers (Thompson et al., 2006). Neither of these models has considered how the presence of different kinds of motion cue might effect the perception of speed. If speed perception for heterogeneous stimulus pairings was shown to exhibit similar contrast dependencies, as has been demonstrated for homogeneous pairings, it would suggest that any computational models of speed processing would have to incorporate the capacity for the integration or comparison of chromatic and luminance information in the estimation of stimulus speed.

3.2.2. Results and discussion

Fig. 4 shows the results from the heterogeneous speed matching experiment. Data are shown for two observers for speed matches made between the luminance reference stimulus and a similar test stimulus as well as L/M and S/(L + M) isoluminant chromatic test stimuli. The reference was set at a 5× threshold achromatic grating which moved at a speed of 2 deg/s, with the test grating being modulated along luminance, L–M or S − (L + M) axes in colour space. As in the previous experiment all stimuli were equated in terms of multiples above motion detection threshold.

Several studies have shown that the motion of coloured stimuli may be perceived differently to that of luminance stimuli. In particular, isoluminant chromatic motion is reported as being slower than luminance motion presented at the same rate with equivalent contrast (Cavanagh, Tyler, & Favreau, 1984; Nguyen-Tri & Faubert, 2002). However, from Fig. 4 it can be seen that at test/contrast ratios close to unity there is a close degree of correspondence between the speed matches made for colour and luminance stimuli, there is no evidence of any reduction in the perceived speed of chromatic motion. This suggests that when moving chromatic and luminance stimuli are equated in terms of their respective motion detection, as opposed to their pattern detection thresholds, inequalities between the two types of motion stimuli are removed and psychophysical performance reaches comparable levels (see also Cropper, 1994). This issue has also been raised by Dougherty et al. (1999) who demonstrated that there are differences between the relative sensitivities of colour and luminance revealed by detection thresholds as opposed to the relative sensitivities revealed by speed judgements. This finding, they argue, implies that the neural mechanisms that underpin the visibility of stimuli are very different to those that are involved in the computation of speed. It has been suggested that the chromatic signals conveying motion information have some form of restricted access to area MT/V5 where motion computations are performed (Seidemann et al., 1999). However, once they reach neurons in this cortical region, comparisons of neural activity and psychophysical performance reveal similar sensitivity for chromatic and luminance motion (Barberini et al., 2005). Thus, previously reported differences in the perception of motion of chromatic and luminance stimuli may be a reflection of this difference in accessibility of the respective signals reaching MT/V5, and in certain respects this echoes earlier ideas regarding chromatic motion stimuli being equivalent to low contrast luminance motion stimuli (Troscianko & Fahle, 1988).

As can also be observed in Fig. 4 the contrast dependencies, given by the slopes of the regression lines, are remarkably similar across the different conditions. It would appear that similar misperceptions of speed are made between moving stimuli of similar visibility regardless of their respective contrast composition. This implies that if the operation of a contrast normalisation process that takes place over a wide spatial extent does indeed account for the errors in speed perception, then such a mechanism must

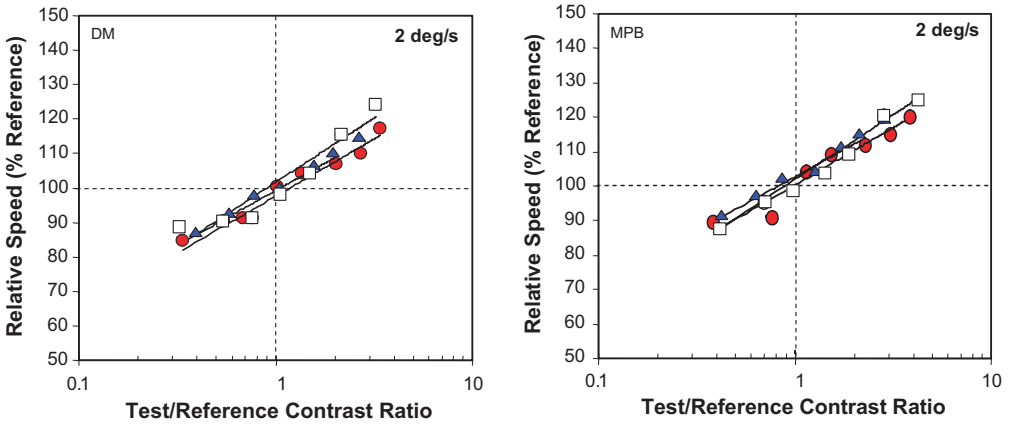

Fig. 4. Speed matching data for homogeneous and heterogeneous combinations of reference and test stimuli. In each case the reference stimulus consists of a luminance grating of speed = 2 deg/s which was combined with either a luminance (squares), L/M (circles) or S/(L + M) (triangles) test stimulus. Observers DM and MPB.

be able to average across both colour and luminance contrast. Obviously, if such averaging can take place it argues against speed perception being based upon segregated colour and luminance input, there must be the capability to pool information across these sub-modalities. However, whilst contrast normalisation might satisfactorily explain the kinds of errors in the perception of speed in speed matching experiments like these, it has certain shortcomings when it comes to explaining other speed misperceptions (Thompson et al., 1996), for example those induced by proximal 'modifier' stimuli (Smith & Derrington, 1996). In the next experiment we wished to examine the extent of interaction between chromatic and luminance motion under these conditions.

4. Modifier speed matching

4.1. Introduction

Smith and Derrington (1996) have previously shown that the perceived speed of a grating can be influenced by 'modifier' gratings in close spatial proximity to the test stimuli. They found that the speed misperceptions induced in the test stimuli by the higher contrast modifiers were dictated by the temporal properties of the modifier stimuli. If the modifiers moved faster than the test stimulus, then the test was perceived as moving faster than its actual speed, whilst if they moved more slowly, the test was perceived as moving slower than its actual speed. This pattern of results was explained by the fact that the addition of a high contrast modifier led to an increase in the motion energy input most sensitive to the modifiers' temporal frequency which thereby led to a shift in the perceived speed of the test grating closer to the modifier.

In this series of experiments we wished to examine whether the contrast composition of modifier stimuli (i.e. chromatic or luminance) had any influence on the pattern of results reported by Smith and Derrington (1996). Could, for example, chromatic isoluminant modifiers bias the perceived speed of achromatic contrast test stimuli, and vice versa. If the induced misperceptions of speed turned out to be the same regardless of the contrast composition of the modifier and test stimuli, it would be evidence to support the idea that speed perception is based upon a mechanism which pools motion energy from different inputs and the nature of those inputs (chromatic or luminance) is ignored. But, on the other hand, if luminance modifiers had no influence on chromatic speed perception (and vice versa) this would imply segregation of chromatic and luminance contrast in the computation of speed.

4.2. Results and discussion

The data shown in Fig. 5a replicate the major findings of Smith and Derrington (1996) for a luminance test stimulus moving at 8 deg/s in the presence of luminance modifier stimuli, in that the test stimulus appears to move faster when the modifiers move faster and is perceived to move more slowly when the modifiers are slower. In addition, we also show that when the modifier stimuli consist of either L/M or S/(L + M) isoluminant gratings, the same results are produced for the luminance test stimulus. The data in Fig. 5a were obtained with a relatively fast moving grating stimulus (8 deg/s). However, it is at slower stimulus speeds (<4 deg/s) where it has been suggested that there is a segregation of colour and luminance contrast processing in the analysis of moving stimuli (Hawken et al., 1994). Therefore we performed a similar modifier speed matching experiment but in this instance with a slower moving test stimulus (3 deg/s). The results of this experiment are shown in Fig. 5b and are similar to those obtained for the faster stimuli. Once again the perceived speed of the luminance test stimulus can be altered by the speed of modifier stimuli and that these biases occur regardless of whether the modifiers are achromatic, L/M or S/(L + M) gratings. In a control experiment we investigated the effect the test and reference chromaticity would have on speed matching. In order to ascertain that the effects were not conditional upon test-reference modulation, we repeated the experiment with the test and reference modulated along the L/M axis (see Fig. 5c and d) and found a similar pattern of results as obtained with the achromatic test and reference stimulus condition. We can conclude that the modifier effects are not dependent upon either the modifier or test-reference modulation.

The effects of modifier stimuli on speed perception, described above, were obtained for modifiers of relatively high contrast. We were interested in examining to what extent similar effects could be generated by low contrast modifier stimuli. In particular, we wanted to know whether low contrast, slowly moving luminance modifiers could influence the perceived speed of chromatic stimuli and vice versa. Our earlier experiments on the contrast dependency of speed perception, like other studies (Burr et al., 1998; Hawken et al., 1994), highlighted the existence differences between colour and luminance stimuli. This has been interpreted as evidence in favour of separate processing pathways for chromatic and luminance stimuli of low contrast and low speed (e.g. Derrington et al., 2004). We therefore wanted to assess whether the existence of potentially different processing substrates would preclude interactions between low contrast, low speed modifier and reference stimuli with different chromatic and luminance contrast composition.

Fig. 6 shows how the magnitude of the perceived change of reference speed varies as a function of modifier stimulus contrast. In this experiment the L/M reference stimulus moved at a speed equal to 3 deg/s whilst the modifiers moved at a slower speed of 0.75 deg/s (hence the percentage change shown indicates how much the perceived speed is slowed down in comparison to the true reference speed). As one might expect the effect of the modifiers on perceived speed increases as they increase in contrast, but it is interesting to note that even at low contrast levels (<5× thresh-

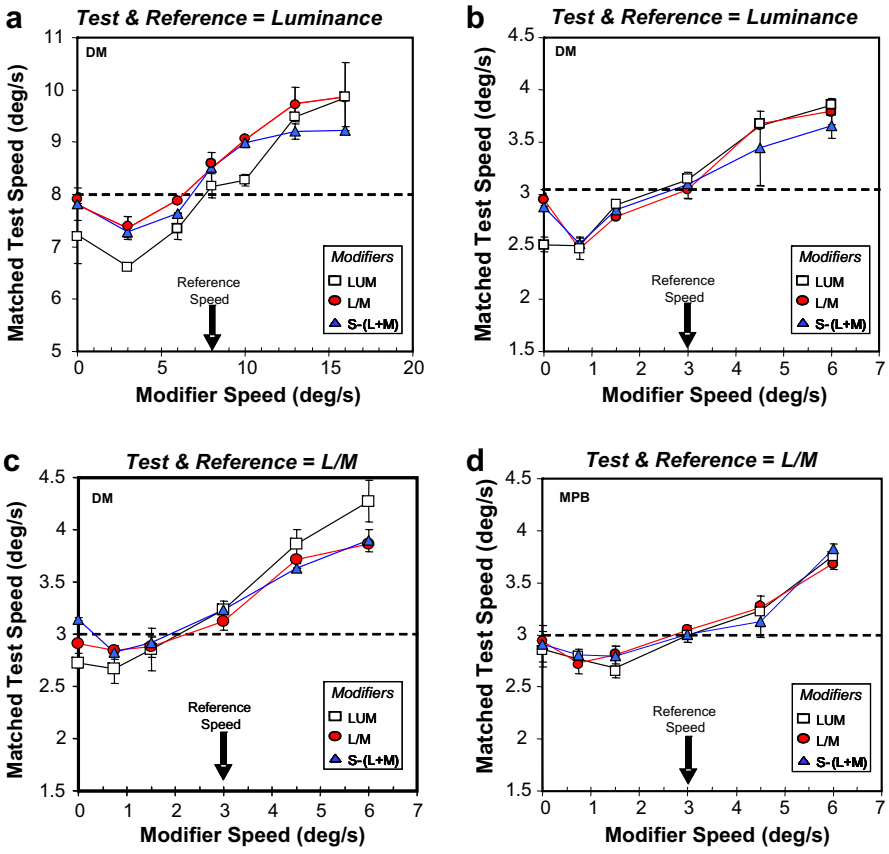

Fig. 5. Modifier speed matching data for reference stimuli of speed 8 deg/s (a) and 3 deg/s (b). In A and B the reference and test stimuli are luminance gratings with speed matches being made in the presence of luminance (squares), L/M (circles) or S/(L + M) (triangles) modifier stimulus. Error bars represent ± 1 standard deviation of the mean. (c) and (d) show similar matching functions for observers DM and MPB when the test and reference stimuli are L/M gratings of speed = 3 deg/s. As in (a) and (b) speed matches were made in the presence of luminance, L/M and S/(L + M) modifiers.

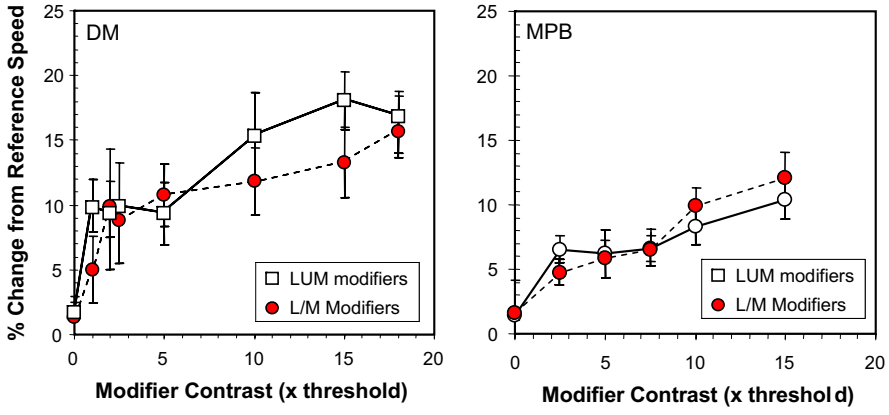

Fig. 6. Variation in the perceived change of reference stimulus speed as a function of modifier contrast. The data are for an isoluminant L/M reference stimulus moving at a true speed of 3 deg/s in the presence of either luminance (squares) or chromatic (circles) modifiers moving at a slower speed of 0.75 deg/s. Data are shown for two observers DM and MPB. Error bars represent ± standard deviation.

old) there is still a robust influence on speed perception for both chromatic and luminance contrast modifiers. The results demonstrate that even though low contrast and low speed chromatic and luminance motion stimuli are purported to be segregated, in terms of their respective processing mechanisms, the extent of this segregation cannot be absolute as they still have the potential to interact and influence one another in the context of speed perception.

From the foregoing experiments it is evident that the perceived speed of sinusoidal gratings can be altered by the addition of adjacent modifier gratings and their effects are the same regardless of whether they comprise

chromatic or luminance contrast. Speed misjudgements were observed when the modifiers moved both faster and slower than the speed of the reference grating. The effect is simply described by a faster modifier leading to an overestimation in perceived speed, with a slower modifier leading to an underestimation in perceived speed, an effect independent of stimulus chromaticity. It can be deduced that the temporal properties of the high contrast grating are being superimposed upon the reference stimuli, leading to misperceptions of speed. This is consistent with the idea that speed is encoded by the relative activities of temporal filters (Adelson & Bergen, 1986)—band pass and low pass temporal filters. The presence of the high contrast modifier grating in close proximity to the reference grating selectively increases the energy input to the temporal filter closest to the modifier's temporal frequency, thereby pushing the perceived speed of the reference grating closer to that of the modifier. As the effect on the reference is independent of stimulus chromaticity, this points to a speed mechanism which is insensitive to the contrast composition of inputs and can pool motion energy over a relatively large spatial extent.

The data in Figs. 7 and 8 show how the influence of the modifiers varies as a function of separation from the reference stimulus in space and time, respectively. In both experiments the modifiers were high contrast chromatic (L–M) or luminance gratings moving at 6 deg/s (8× threshold), whilst the test and reference stimuli were L/M gratings of speed equal to 3 deg/s at a contrast of 5× threshold. Not surprisingly, the data demonstrate that the modifiers have their greatest effect on the perception of speed when they are close in space and time to the presentation of the reference stimulus. However, it clear that there is an extended spatio-temporal window across which the modifiers are able to exert an influence on perceived speed. Furthermore, the extent of this window is the same for both chromatic and luminance contrast. For increasing spatial separations the data in Fig. 7 can be fitted by a single exponential function which gives a mean spatial decay constant of 3.10° for the luminance modifiers and 3.17° for the chromatic modifiers. For temporal separations between the modifiers and reference stimuli (Fig. 8), exposure of the former up to 3–4 s prior to the onset of the latter can still produce a measurable effect on perceived speed (mean time constants: luminance = 2.72 s, chromatic = 3.41 s). Even presentation of the modifiers after the appearance of the reference, prior to the observer making their response, still can modify perception. However, the temporal extent of this influence is more limited with the decay of this effect is approximately twice as rapid as that for exposure of the modifier prior to reference onset (mean time constants: luminance = 1.5 s, chromatic = 1.7 s).

Clearly, the neural processes that underpin the perception of speed are susceptible to manipulation across a relatively broad spatial and temporal window. The extended range of effects would suggest that these processes are located in a cortical region lying beyond area V1. The

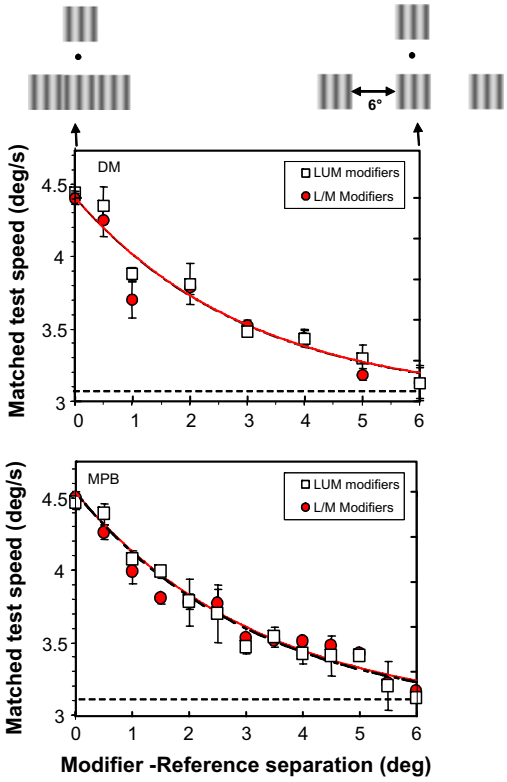

Fig. 7. Data showing the effect of increasing spatial separation between the modifier and reference stimuli. In each case the test and reference stimuli were luminance gratings of speed = 3 deg/s. The modifier stimuli moved at a speed = 6 deg/s and could be either luminance or L/M chromatic gratings. The perceived increase in speed induced by the modifiers falls from a maximum, when the separation is zero, to levels similar to those made in the absence of modifiers (dotted line) when the separation is greater than 6°. The luminance and chromatic data have been fitted by a single exponential decay function which gives spatial decay constants: DM lum = 3.2°, chrom = 3.0°; MPB lum = 3.3°, chrom = 3.1°.

spatial range of modifier influence on speed operates over an extent greater than that normally expected for V1 receptive field sizes, which are typically smaller than 1° (Dow, Snyder, Vautin, & Bauer, 1981), but are easily encompassed by receptive field sizes that have been documented for area V5/MT (e.g. Felleman & Kaas, 1984). Similar effects with increasing spatial separation have also been demonstrated in a visual working memory task based upon direction discrimination (Zaksas, Bisley, & Pasternak, 2001). Visual memory mechanisms may also provide an explanation for the extensive temporal range over which the modifiers are able to influence speed estimates. The visual system has an excellent ability to retain information about stimulus speed over time. Magnussen and Greenlee (1992) have shown that short term visual or working memory for speed is highly accurate for inter stimulus intervals of up to 30 s. Of particular relevance to the results reported here is the fact that the accuracy of this stored memory can be disrupted by the presentation of intervening masking stimuli which can lead to a reduction in speed discrimination ability (Magnussen & Greenlee, 1992). It is tempting

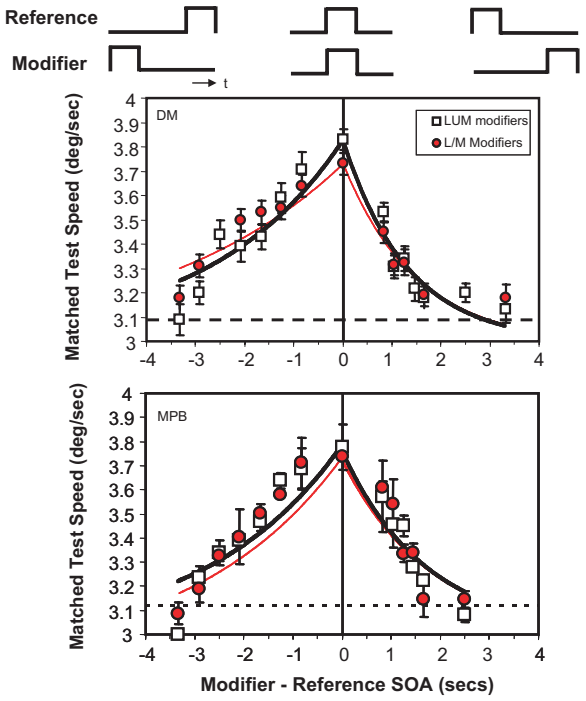

Fig. 8. Data showing the effect of increasing temporal separation between the modifier and reference stimuli. Test, reference and modifier stimuli were the same as those used in Fig. 7 except that the modifiers were presented either prior to (−ve SOA) or after (+ve SOA) the presentation of the test and reference stimuli. SOA = 0 represents the simultaneous presentation of test and modifier at which the modifiers induced their maximum effect on perceived speed. As in Fig. 7 the data have been fitted by a single exponential decay function which gives temporal decay constants for: (i) presentation of modifiers prior to the reference, MPB lum = 2.77 s, chrom = 3.02 s; DM lum = 2.66 s, chrom = 3.8 s. (ii) presentation of modifiers after the reference: MPB lum = 1.67 s, chrom = 1.89 s; DM lum = 1.32 s, chrom = 1.5 s.

to speculate that similar mechanisms might be operating in the temporal separation effects reported above. If visual short term or working memory processes are involved in the generation of these extended spatial and temporal modifier effects, it is interesting to note that area V5/MT and has also been shown to play an important role in the retention of sensory information about object motion (Bisley & Pasternak, 2000; Bisley, Zaksas, Droll, & Pasternak, 2004; Campana, Cowey, & Walsh, 2002).

5. General discussion

In this series of experiments we have investigated errors that can be made by the human visual system in the estimation of stimulus speed, and in particular how these errors depend upon the chromatic and luminance contrast composition of the stimuli. Prompted by discrepancies between studies that have reported on the one hand, differences between the contrast dependencies of speed perception for chromatic and luminance motion (Hawken et al., 1994), and those on the other which have found no difference between the two types of motion (Dougherty et al., 1999), we re-examined speed matching performance for colour and luminance stimuli equated with reference to their respective motion detection thresholds. We have found that whilst there may indeed be differences between the variation with contrast for colour and luminance speed perception, these differences are only apparent for a relatively restricted range of stimulus conditions. Our results suggest that the extent of segregation between colour and luminance speed perception for slowly moving stimuli is not as distinct as have been reported previously (Hawken et al., 1994), and only occurs for slowly moving stimuli that are close to motion detection threshold (<5×). The separability between colour and luminance stimuli, in terms of their respective speed gains, becomes less distinct at faster rates and at higher supra-threshold contrasts. The idea of strict segregation also has to be challenged in the light of interactions shown in this study to occur between colour and luminance information in the generation of speed misperceptions. The modifier speed matching experiments, in particular demonstrate the equal capacity of colour and luminance motion in distorting the perceived speed of a moving reference stimulus. These distortions even occur with low contrast low speed modifiers where the segregation between colour and luminance stimuli should be most apparent. This clearly shows that the visual system is able to combine different kinds of motion cue during the neural processing that determines the perception of stimulus speed.

5.1. Implications for models of speed perception

A number of different computational models of speed perception have been suggested which have variously depended upon: the calculation of motion energy (Adelson & Bergen, 1985; Watson & Ahumada, 1985), the response frequency of cortical neurons (Barlow & Hill, 1963; Bex, Bedingham, & Hammett, 1999; Clifford & Langley, 1996) and Bayesian models (Weiss, Simoncelli, & Adelson, 2002). However, many have struggled to account for the fundamental observation that speed perception is not contrast invariant. Ratio models, in their various guises (e.g. Adelson & Bergen, 1986; Metha & Mullen, 1997; Stone & Thompson, 1992; Thompson et al., 2006), have attempted to account for this property of speed perception with varying degrees of success. But what is apparent from this study is that future models of speed perception have to be able to account for two other important additional factors. The first is that speed perception would appear to involve the integration of colour and luminance information. The conflicting views in the literature regarding the integration of colour and luminance information in the perception of motion might be accounted for by the fact that in the early stages of motion processing in the cortex (i.e. pre V5/MT) segregation between colour and luminance is maintained to a large extent. Psychophysical evidence points to the existence of separable low-level colour and luminance

motion pathways (Cropper & Derrington, 1994, 1996; Derrington & Badcock, 1985; Krauskopf & Farrell, 1990; McKeefry et al., 2006; Willis & Anderson, 1998). At higher levels in the motion pathway (V5/MT and beyond) initially segregated colour and luminance inputs could be combined to allow more complex computations involving moving stimuli, such as their speed and position estimates, for example, to take place without regard to the contrast composition of the stimulus (Chichilnisky, Heeger, & Wandell, 1993; Dougherty et al., 1999; McKeefry et al., 2006). Area V5/MT represents a good candidate for the locus where chromatic and luminance information can be combined in the perception of stimulus speed for two reasons; firstly, because it contains neurons that are responsive to both kinds of motion (Barberini et al., 2005; Dobkins & Albright, 1994; Gegenfurtner, Kiper, Beusmans, Carandini, & Zaidi, 1994; Saito, Tanaka, Isono, Yasuda, & Mikami, 1989; Seidemann et al., 1999; Thiele, Dobkins, & Albright, 1999, 2001). V5/MT appears to be capable of processing perceptually relevant motion signals for all stimulus types, including chromatic ones (Barberini et al., 2005; ffytche, Skidmore, & Zeki, 1995). Second, lesion (Newsome, Wurtz, Dursteler, & Mikami, 1985; Orban, Saunders, & Vandenbussche, 1995), electrophysiological (Liu & Newsome, 2005) and neuroimaging (Chawla, Phillips, Buechel, Edwards, & Friston, 1998; Huk & Heeger, 2000) studies have all highlighted the prominent role that area V5/MT plays in the analysis of stimulus speed. The idea of integration across visual sub-modalities is also implicit in current physiological models which propose that the perception of the speed of moving stimuli is based upon neurons that are selectively tuned to different speeds but are insensitive to other stimulus attributes such as their pattern composition (Perrone & Thiele, 2001). We might also now predict, on the basis of our psychophysical results, that these neurons also ignore the chromatic attributes of the stimulus.

The second factor that has to be taken into consideration in future models is that the mechanisms that govern speed perception have a broad spatial and temporal sampling window across which they can be influenced and their outputs altered. With respect to spatial interactions the importance of analysing moving stimuli across a wider spatial context, beyond that of the stimulus itself, has been a fundamental component of earlier models (Smith & Derrington, 1996; Stone & Thompson, 1992; Thompson et al., 1996). In terms of interactions between moving stimuli over time, an appreciation of the temporal dynamics of speed processing can be found in models of how speed perception varies following motion adaptation (Hammett, Thompson, & Bedingham, 2000; Hammett, Champion, Morland, & Thompson, 2005). This model highlights ideas that are central to our study, namely, that the perception of speed of a moving stimulus is highly dependent upon the context in which it is viewed and can be influenced by prior viewing conditions.

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